Color-Vision Mechanisms in the Peripheral Retinas of Normal and Dichromatic Observers

B. R. WOOTEN and GEORGE WALD

From the Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138. Dr. Wooten's present address is Department of Psychology, Brandeis University, Waltham, Massachusetts 02154.

ABSTRACT It is possible that so-called normal trichromatic vision occurs only between the central blue-blind fixation area and about 30° peripherally. Beyond about 30° vision has been alleged to become dichromatic (red-green blind), and beyond about 60°, monochromatic. Hence every form of color blindness may characterize various zones of the normal retina. We have studied mechanisms of peripheral color vision, mainly by measuring the spectral sensitivities of the blue-, green-, and red-sensitive systems, isolated by differential color adaptation. In normal observers the sensitivity of the blue-mechanism falls off about 2 log units by 80° out. The green- and red-sensitive systems decline only about 0.7 log unit over the same range. Protanopes, deuteranopes, and tritanopes exhibit comparable changes. We have not found any color mechanism present centrally to be wholly lost peripherally. Nor, for dichromats, have we found any mechanism missing centrally to be present peripherally. Whatever evidences of peripheral color blindness have been observed appear to involve other mechanisms than failure of receptors, probably including some fusion of neural pathways from receptors to centers.

INTRODUCTION

Using an extension of Stiles's two-color threshold method (1949, 1959), Wald (1964, 1966) has measured the spectral sensitivities of the three classes of cone in human observers. By appropriate choices of continuous, brilliant colored backgrounds, it is possible so to depress the sensitivities of two of the three color mechanisms that the increment threshold for a small field is determined mainly by the third. Exposure to an intense yellow background, for example, so light-adapts the green- and red-sensitive systems while sparing the blue-sensitive system that increment thresholds measured on the yellow background are governed almost entirely by the blue-sensitive system.[1]

[1] Our terms, though arbitrary, are no more so than previous terms. Like much other scientific terminology this one is not to be taken literally; one has to know what it means. The three cone photopigments that govern primate color vision, and the neural mechanisms that they individually

Similarly adaptation to wave bands in the blue and red, i.e. a brilliant purple background, isolates mainly the green-sensitive system; and adaptation to a bright blue background isolates primarily the red-sensitive system. After correction for the spectral transmission of the ocular media, the spectral sensitivities of the three cone systems so obtained agree well with the absorption spectra of the cone pigments measured by direct microspectrophotometry (Marks, Dobelle, and MacNichol, 1964; Brown and Wald, 1963, 1964).

Using this procedure, Wald (1967), reexamining older reports that much of the central fovea in normal subjects may be blue-blind (König and Köttgen, 1894; Willmer, 1944; Willmer and Wright, 1945), found that in 8 of 11 observers a small central area of the normal fovea—the fixation area—about 8 min in diameter, appears wholly to lack blue-sensitive cones, and hence is tritanopic in the classic sense. This finding recalled old reports that the normal peripheral retina beyond 20°–30° from the fixation point behaves as though red-green blind, and beyond about 60°–70° behaves as though totally color-blind. It seemed possible therefore that what is regarded as normal trichromatic vision occurs only in a broad central annulus between the blue-blind fixation area and about 20°–30° out; and that all the classic forms of color blindness, including total color blindness, occur in various, roughly concentric zones of the normal retina (Wald, 1967).

The present experiments inquire into possible mechanisms underlying color blindness in the peripheral human retina. Using the method of selective adaptation, we have singled out the cone mechanisms and measured their relative sensitivities out to 80° from the fixation point, in normal observers and congenital dichromats. It emerges that every class of cone present in the fovea occurs also throughout this extent of the peripheral retina. Color blindness in the peripheral retina, to the extent that it occurs, has some other basis than lack of one or more of the cone mechanisms.

First, the phenomena. In order to understand the observations, one must recognize that red-blinds and green-blinds (protanopes and deuteranopes) see only two hues in the spectrum, blue and yellow, separated by neutral points that can be matched with white at about 493 and 497 nm, respectively. Blue-blinds (tritanopes) see only green and red, with a neutral point at about

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excite we call blue-, green- and red-sensitive (*B*, *G*, *R*), though each of them is sensitive to wide reaches of the spectrum. Similarly the terms red-, green-, and blue-blind imply only the absence or functional failure of one of these three systems, and hence are synonymous with the traditional terms protanope, deuteranope, and tritanope. Red-green blindness is a behavioral term, involving the incapacity to differentiate in hue wavelengths longer than about 495 nm; or, said otherwise, the ability to match all wavelengths from green to red with yellow. Protanopes and deuteranopes are red-green blind owing to loss of the red- or green-sensitive system (Wald, 1966), but red-green blindness could result also from fusion of the red- and green-sensitive mechanisms, as appears to be the case in the human peripheral retina.

577 nm. Such perceptions have been reported since the first description of red-blindness—his own—by Dalton (1798); and any doubts that they are real are resolved by observations on more than 40 uniocular dichromats—persons with one trichromatic and one dichromatic eye—who with their normal eye can check reliably the sensations experienced with the color-blind eye (Judd, 1949; Graham and Hsia, 1958).

Purkinje (1825) may have been the first to note that colored objects change in hue when viewed askance and may look completely colorless in the far periphery. Many investigators have subsequently studied the peripheral color zones (cf. especially Aubert, 1857, 1865; Landolt and Charpentier, 1878; Bull, 1881, 1895; Hess, 1889; Abney, 1893, 1913; Ferree and Rand, 1919; Rinde, 1932), with somewhat conflicting results, associated in large part with the nature of the stimulus. In general the brighter, larger, and more saturated a colored stimulus, the wider the field in which it excites about the same hue sensation as centrally. Nevertheless most investigators agree that as colored stimuli are moved outward from the fovea, reds and greens cease to be discriminated and tend to look yellow, violets and blues to look blue beyond 20°–30°, and all to look colorless beyond about 60°–70° excentrically. That is, the central zone out to 20°–30° behaves as though trichromatic, the middle periphery to 60°–70° as though red-green blind, and the extreme periphery as though achromatic.

Recent studies tend to support these observations. Moreland and Cruz (1959) determined the mixtures of red, green, and blue primaries in a foveal field that matched monochromatic stimuli at various peripheral loci. They found strong dichromatic tendencies beyond 25°–30° and monochromacy beyond 40°–50°. Boynton, Shafer, and Neun (1964) examined the color naming of monochromatic stimuli at 0°, 20°, and 40° out. They found a marked reduction in red and green responses at 40° out.

The mechanisms of color blindness also raise problems. In general two kinds of mechanism are in question: conditions in which one or more of the three types of cone are absent (loss mechanisms); and conditions in which, though all three types of cone are present, their excitations are conveyed centrally by fewer than three channels (fusion mechanisms).[2] Though the

[2] Another possibility of course is pigment mixture in the cones rather than neural fusion. The mechanism that segregates the three cone photopigments in three classes of cone—as, at least to a first approximation they are segregated in primate parafoveal cones (Marks, Dobelle, and MacNichol, 1964; Brown and Wald, 1964)—is altogether unknown. Every cone presumably possesses the genes for synthesizing all three cone opsins, which combined with 11-*cis* retinal could make all three cone photopigments. It is not impossible that the segregating mechanism operating in the central retina fails to keep the green- and red-sensitive pigments apart in the mid-periphery, and is completely in abeyance in the far periphery. It should be clear that our selective adaptation procedure would within limits succeed in distinguishing the individual photopigments even when mixed in single cones.

possibility was entertained that both mechanisms might operate in hereditary human color blindness—particularly in deuteranopes (Wald, 1964)—analysis by the color adaptation procedure revealed only loss mechanisms (Wald, 1966). Protanopes appear to lack functional red-sensitive cone pigment and hence presumably red-sensitive cones, deuteranopes the green-sensitive cones, and tritanopes the blue-sensitive cones. Also the blue-blindness of the fixation area in the normal fovea appears to go with the lack of functional blue-sensitive cones. Similarly congenital total color blindness in all cases so far examined appears to involve the function of only one type of cone, or the absence of all normal cone function (Pitt, 1944; Weale, 1953 *a*; Sloan, 1954; Alpern, Falls, and Lee, 1960; Blackwell and Blackwell, 1961; Alpern and Spivey, 1965).

The present experiments, since they demonstrate the operaion of all three visual pigments up to 80° excentrically, suggest that fusion mechanisms are the main source of the red-green blindness of the near periphery and the total color blindness of the far periphery of the normal retina.

METHODS

Apparatus

Fig. 1 is a diagram of the two-channel Maxwellian view system used in all these experiments. The image of the source S_1, a 45 watt tungsten-iodine lamp, was focused by a lens (L_1) on the entrance slit of the grating monochromator (MONO; Bausch and Lomb, Inc., Rochester, N. Y.). The monochromatic light emerging from the exit slit was collimated by L_2 before passing through a pair of counterbalanced circular neutral wedges (W). Additional attenuation could be provided with neutral filters placed at F_1. A circular aperture (A_1) defined the 1° test field and L_3 then cast an image of S_1 on an adjustable slit (SL_1). An electromechanical shutter (SH), placed before SL_1, provided for the test flash. L_4 recollimated the beam, and L_5 threw the final image of the filament into the plane of the observer's pupil.

Light for the background field was provided by the same source (S_1). L_6 collimated the beam that passed through color filters placed at F_2. A circular aperture (A_2) defined the 14° background field. L_7 formed an image of S_1 on adjustable slit SL_2. After collimation by L_8 the beam was rotated 90° by a front-surfaced mirror (M). The background was then combined with the test channel by reflection from a thin quartz coverslip (BS).

The final lens (L_5) in the system so formed a pair of superimposed filament images limited in size by slits SL_1 and SL_2 to 1 mm width and 4 mm length. When the observers were positioned so that the final filament images were centered within the pupil they saw a 1° test flash superimposed at the center of a 14° background.

Foveal fixation was achieved by inserting a pair of thin, opaque pointers at A_2 so that their tips were 1.5° apart. The test flash appeared centered between these horizontal pointers. For the 7° excentric locus, the tip of a single pointer was positioned on the left side of the background field. For all loci more than 7° out, a self-

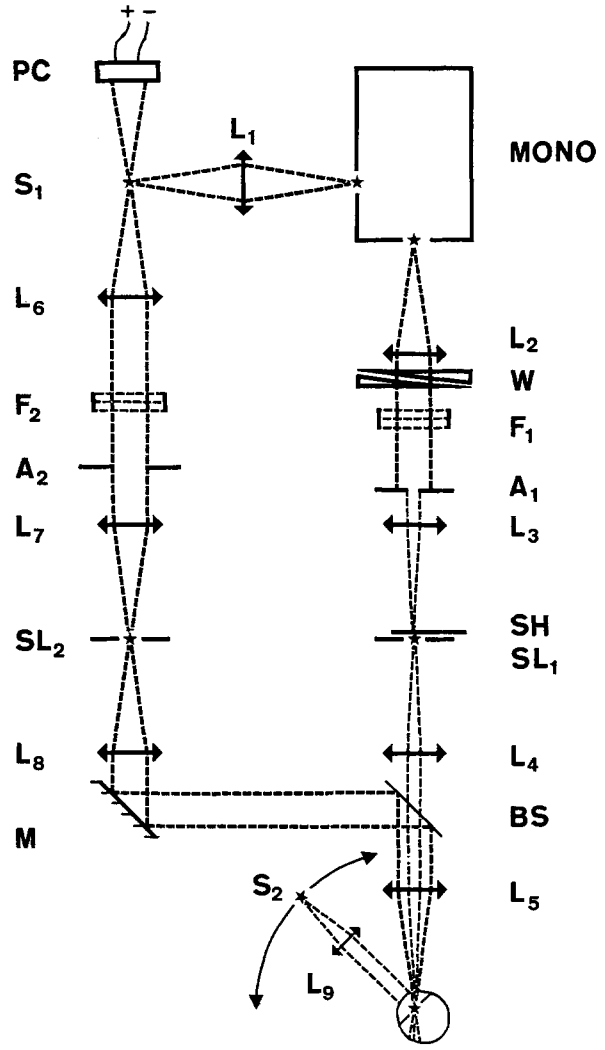

FIGURE 1. Diagram of the optical system, described in the text. Light path of the monochromatic test field on the right, that of the bright colored backgrounds on the left. Both are served by the same light source S_1, monitored by photocell *PC*. Both the 1° test field and 14° background are seen in Maxwellian view. During a run the background is on continuously, the test field superimposed on it for flashes of 180 ms.

luminous fixation point was provided by a grain-of-wheat lamp (S_2) viewed through a focussing lens (L_9). The observers could control the brightness of S_2 and were instructed to keep it "dim but distinct."

L_1 through L_5 were quartz lenses; L_6 through L_9 were achromatic glass lenses.

With the type of optical system outlined above it is essential, particularly with peripheral loci, to hold the observer's head rigidly in place to make sure that all the light in fact passes through the pupil. This was achieved with a dental-impression

bite-bar and an adjustable forehead rest, both mounted on a sturdy three-dimensional machine movement. The entire assembly, including the fixation unit, was secured to a milling-machine-type rotary table. The various components were adjusted so that the final filament image was at the center of rotation. When the eye was properly positioned for the 0° locus, one could shift to any other locus by simply rotating the rotary table. Thus, when in this paper we refer to various loci in terms of visual angle, we really refer to the angle between the optic axis of the eye and the axis of our optical system.

Calibration

Power for the tungsten-iodine lamp was provided by an AC regulated power supply (Sorensen Operation, Raytheon Co., Norwalk, Conn.). The current (about 6.3 A) was monitored with an ammeter in series with the lamp, and the light output with a photocell (PC) placed near the source. The light output was adjusted when necessary with a variable transformer (Variac, Superior Electric Co., Bristol, Conn.).

The neutral filters and wedges were calibrated at each wavelength with a photomultiplier tube (and associated electronics; Photovolt Corporation, New York) placed at the final filament image. The relative spectral energy for the test channel was determined by placing a photodiode, which had previously been calibrated against a thermopile, at the final filament image. The current output of the photodiode (United Detector Technology Corp., Santa Monica, Calif.) was read by a low-impedance ammeter thus assuring linearity of response. The relative spectral energy distribution was checked periodically, but proved to be quite stable.

The following color filters were used for the background field: *Yellow*: Cornea, 3482 plus a Jena KG1 heat filter. *Blue*: Wratten 47. *Red* and *blue* (purple): two Wratten 34A's. The relative spectral energies produced by these filters at the corning determined with a spectroradiometer (ISCO, Lincoln, Nebraska), are shown in Fig. 2. The retinal illuminance was determined for each field with an SEI photometer

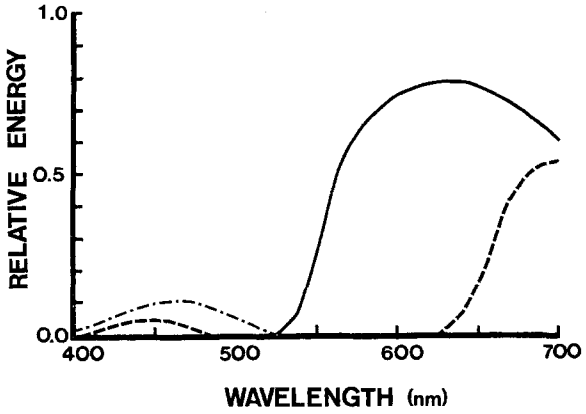

FIGURE 2. Relative energies of bright colored background fields as measured at the observer's cornea. Solid line, yellow background: Corning filter 3482 plus Jena KG 1. Dashed line, purple background: two Wratten 34A filters. *Dot-and-dash line*, blue-green background: Wratten 47 filter.

according to Westheimer's method (1966); the values in log photopic trolands were 5.95 for the yellow, 4.72 for the blue, and 4.07 for the purple background.

The entrance and exit slits of the monochromator were set at 1 mm, resulting in a nominal waveband of 3 nm half-width.

Procedure

The color vision of each observer was assessed with the Ishihara Pseudoisochromatic Plates plus Farnsworth's tritanope test plate, the Farnsworth 15-Hue test, and the Hecht-Shlaer anomaloscope.[3] Two observers (B. W. and M. L.) were normal trichromats, P. O. and B. C. were deuteranopes, J. H. was a protanope, and R. B. was a tritanope. All were under 30 except R. B. who was 45.

All subjects used only the right eye, the left being covered with a black patch. Only the horizontal meridian of the nasal retina was examined. At extreme peripheral loci the pupil presents a small cross-section to the entering beam. To allow the beam to pass unhindered through the pupil at all loci it was dilated before each session by instilling two drops of a mydriatic (Mydriacyl, Alcon Specialty Products, Inc., Moonachie, N. J.) into the observer's eye. This rapidly expanded the pupil to a diameter of about 7 mm, so that even at the 80° locus all the light reached the retina.

The observer was first positioned by adjusting the three-dimensional bite-bar assembly until the final filament image was centered in the dilated pupil for foveal viewing (0°). The test field set at 550 nm was then exposed and optimal focus achieved by moving the field stop (A_1) relative to the lens, L_3. Then the rotary table was adjusted to correspond to a given peripheral locus and the position of the eye was rechecked. After 3 min adaptation to a background color, we began to measure increment thresholds, using test flashes of 180 ms, repeated once every 3 s by means of a function generator (Grass Instrument Co., Quincy, Mass.) coupled to the electromechanical shutter (*SH*). With the monochromator set at a particular wavelength and the wedge set so that the increment flash was from 1 to 0.5 log unit above threshold, flashing was started. The observer signalled that he saw the flash with a single tap (the absence of a tap meant that the flash was not detected). Succeeding flashes were attenuated in steps of about 0.05 log unit until three successive flashes went undetected. The threshold was defined as the luminance of the last "seen" flash preceding three "unseen" ones. This procedure was immediately repeated twice for the same wavelength; the final threshold was taken to be the median of the three determinations. The monochromator was then set at another wavelength and this procedure repeated. Wavelengths were run consecutively from one end of the spectrum or the other. The final spectral sensitivity functions at each locus and for each background represent the mean of two such runs, one beginning at the short-wave end and one beginning at the long-wave end of the spectrum, to counterbalance any serial effects. The observers were required to view the backgrounds continuously until a complete spectral traverse could be made. This took about 20 min.

[3] For the loan of this anomaloscope, built by O. C. Rudolph, we are greatly indebted to the Medical Research Laboratory of the U.S. Submarine Base at New London, Conn.

Each session involved only one background, with measurements usually at two retinal loci.

RESULTS

Normal trichromats

Fig. 3 shows results for two normal observers at the 0° locus. All measurements are expressed as log relative sensitivity (log 1/threshold) in terms of the rela-

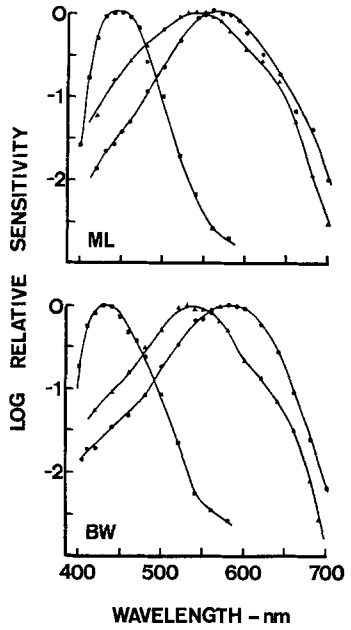

FIGURE 3. Spectral sensitivities of the three color mechanisms in normal trichromats M. L. and B. W., measured in the central fovea. Log relative sensitivities (log 1/threshold) in terms of relative numbers of quanta per flash incident on the cornea. All peak sensitivities have been brought arbitrarily to the same height. *Squares*: blue-sensitive system, measured on yellow background; *triangles*: green-sensitive system, measured on purple background; *circles*: red-sensitive system, measured on blue-green background. These symbols, particularly as they involve the backgrounds, are retained in the remaining figures.

tive numbers of quanta per flash incident on the cornea. Both observers exhibit the expected blue-, green- and red-sensitive mechanisms (*B*, *G*, and *R*), with peak sensitivities at 435–450, 540–550, and 565–580 nm. These results are in good agreement with similar experiments reported previously (Wald, 1964, 1966). Each curve reflects the spectral sensitivity of one cone photopigment in its region of peak sensitivity. It is, however, impossible to isolate a given pigment completely with this procedure. For example the inflection at about 550 nm in the blue-sensitivity function represents residual sensitivities of *G* and *R*. Similarly, the inflection at about 590 nm in the

green-sensitivity function results from the inability to suppress *R* completely. Nevertheless, this color adaptation procedure results in a high degree of isolation of the three cone mechanisms and clearly separates them.

After correcting for prereceptor absorption of light, principally by the lens and macular pigmentation, the main bands of the three mechanisms shown in Fig. 3 agree reasonably well in shape and position with the difference spectra of the foveal photopigments measured microspectrophotometrically, which peak near 440, 540, and 565 nm (Brown and Wald, 1963, 1964; Marks, Dobelle, and MacNichol, 1964).

All the curves in Fig. 3 were brought arbitrarily to the same height to facilitate comparison. The same was done with the measurements at 7° out in Figs. 4 and 5 so that they could better serve as the basis of comparison with the more peripheral measurements. It should be noted however that the actual peak sensitivities measured at the fovea were about 0.5 log unit higher than at 7° out for the red- and green-sensitive systems, and about equal for the blue-sensitive system. After correction for macular pigmentation, which cuts the blue-sensitivity peak about half a log unit at the fovea with little effect upon the other two systems, all three peak sensitivities lie about 0.5 log unit higher at the fovea than at 7° out. This result is consistent with the greater density of cones, presumably of all three types, at the fovea.

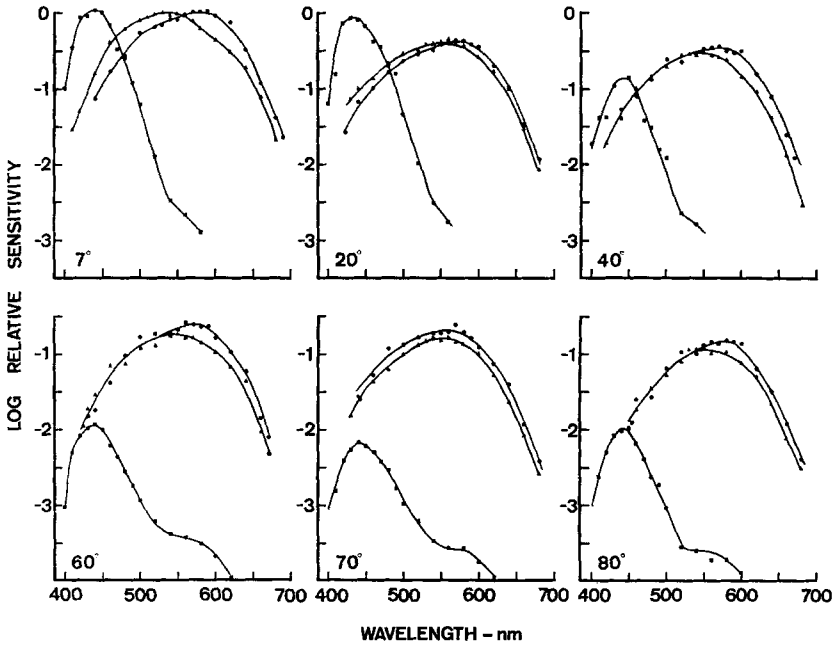

FIGURE 4. Spectral sensitivities of the three color mechanisms in peripheral fields of normal trichromatic observer B. W. The maxima at the 7° locus are arbitrarily brought to the same height: all other curves are relative to these maxima. Symbols as in Fig. 3.

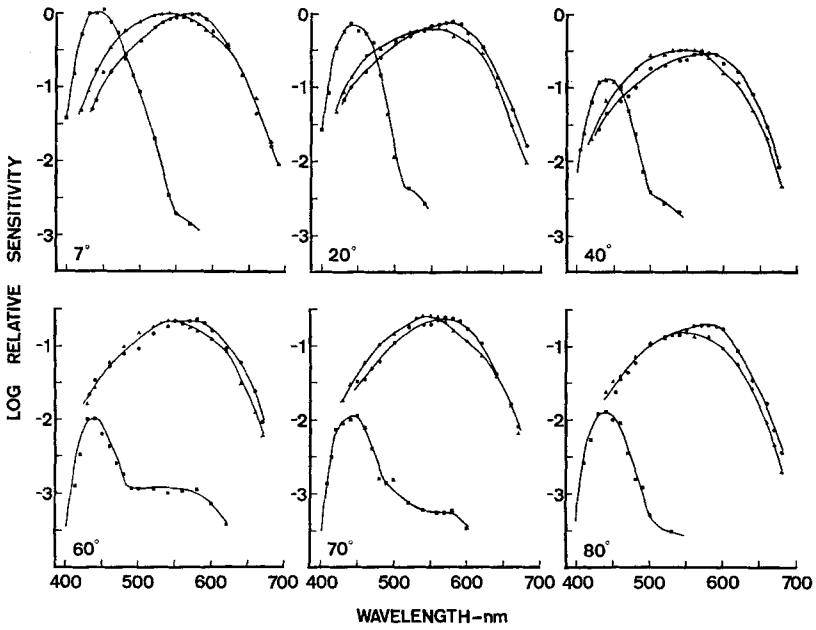

FIGURE 5. Spectral sensitivities of the three color mechanisms in peripheral fields of normal trichromat M. L. Otherwise as in Fig. 4.

Figs. 4 and 5 show measurements on the same two observers at 7°, 20°, 40°, 70°, and 80° in the periphery. It is clear that all three color mechanisms are found at all these loci, but as the field is displaced more peripherally all three cone mechanisms decline in sensitivity, the blue-mechanism much more sharply that the others. At 80° out the green- and red-sensitivity peaks have fallen about 0.7 log unit relative to the 7° locus, but over the same range the blue-sensitivity peak has fallen by about 2 log units. With its great decline in sensitivity peripherally, the blue-sensitive system becomes less well isolated: the "tails" owing to residues of *G* and *R* become more prominent.

The progressive fall in peak sensitivity peripherally relative to the 7° locus is shown in Fig. 6. Relative to the fovea, as already said, the fall in *intrinsic* sensitivity of all three mechanisms is about 0.5 log unit greater. *B* declines most rapidly beyond about 40°, appears to level off at 60°–70°, and increases slightly at the 70° locus. *G* and *R* fall regularly and together to a lowest value at 80° out.

Whereas the blue-sensitivity band at about 440 nm maintains its shape unaltered from 7° outward, the green- and red-sensitivity curves shown in Fig. 4 and 5 tend to grow broader and more poorly separated peripherally. Much of these effects are already apparent at 7° out. At this locus they can be shown to be due to the differential distribution of the macular pigmentation. This is dense within the fovea, where on the average its absorbance is about

0.5 at λ_{max} 455 nm (Brown and Wald, 1963), and is greatly attentuated or absent by 7° out.

Its effects are of two kinds. Since it absorbs mainly below 520 nm, in the fovea it cuts markedly into *G* below this wavelength, and somewhat less into *R*. The result is to narrow both curves in the fovea at short wavelengths, *G* much more than *R*. If the foveal *G* curve is corrected for this filtering effect, it matches *G* at the 7° locus on the short-wavelength side of its maximum; yet on its long-wavelength side the 7° curve still remains broader.

This is because of a secondary effect of the macular pigmentation, on the efficacy of our purple background light in isolating *G* from *R*. This background was designed originally for use in the fovea. Outside the macula, i.e. in the absence of macular pigmentation, more of its blue component penetrates to the cones. Hence it ceases to spare *G* relative to *R* as effectively as in the fovea, and so no longer separates these mechanisms as efficiently. Their partial fusion results in such a broadening of *G* as we observe (Fig. 7). By the

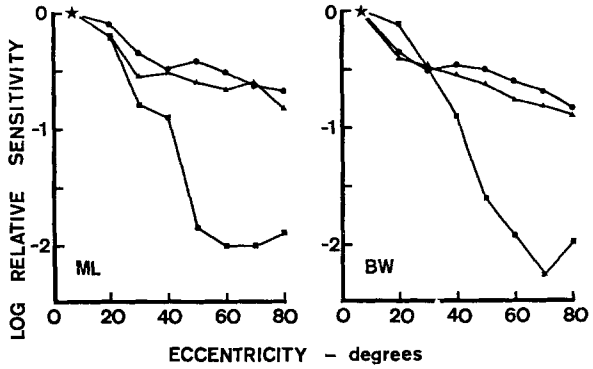

FIGURE 6. Relative peak sensitivities of the three color mechanisms in peripheral fields of normal trichromats M. L. and B. W., taken from Figs. 4 and 5. The peak sensitivities had been arbitrarily equated at the 7° locus. Symbols as in Fig. 3.

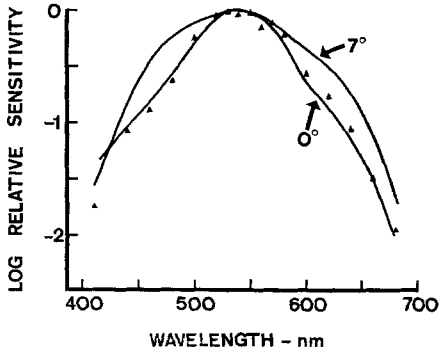

FIGURE 7. Solid lines: Spectral sensitivities of the green-mechanism in the central fovea (0°) and at 7° in the periphery. Triangles: the measurements at 7° out repeated with a xanthophyll filter in front of the eye, simulating the macular pigmentation.

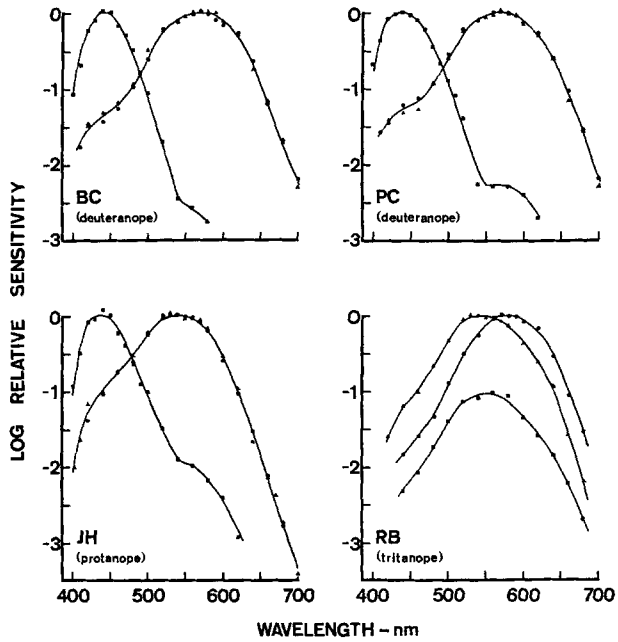

FIGURE 8. Spectral sensitivities of the color mechanisms measured in the central foveas of congenital dichromats. Symbols as in Fig. 3. Two deuteranopes possess only the blue- and red-sensitive systems; one protanope only the blue- and green-sensitive systems; and the tritanope only the green and red-sensitive systems. The attempt to find the blue-sensitive system in the tritanope yields only a composite green-red curve at a lower level of sensitivity (squares). In each case the peaks of the sensitivity curves—except for this last curve—have been arbitrarily brought to the same height.

same token the blue background used to isolate *R* is somewhat intensified in the absence of macular pigmentation, and so works at least as well in the periphery as foveally.

That this is the correct explanation for the broadening of *G* at 7° is shown by the following experiment. The human macular pigment is the carotenoid lutein or leaf xanthophyll, $C_{40}H_{54}(OH)_2$ (Wald, 1945). A liquid filter of xanthophyll was prepared that matched closely in spectrum and depth the average human macular pigmentation at the fovea (Brown and Wald, 1963).[4] Measurements of *G* at the 7° locus with this filter before the eye match in shape and position such measurements made in the fovea without the xanthophyll filter (Fig 7). We can conclude that the difference in shape of *G* and *R* in the fovea and at 7° out are caused by the differential distribution of the macular pigment.

[4] We are indebted to Paul K. Brown for preparing this filter. It consists of a solution of crystalline leaf xanthophyll in a mixture of carbon disulfide and chloroform (20:80), in an absorption cell. The xanthophyll had been heat-isomerized previously by melting the crystals, so as to yield a mixture of *cis* and *trans* isomers, the absorption spectrum of which in this solvent resembles closely that of the macular pigmentation (Brown and Wald, 1963). The absorbance at λ_{max} 455 nm was 0.49.

This factor, however, cannot be invoked to explain a further broadening and loss of isolability of *G* and *R* at higher eccentricities. The course and causes of these further changes are discussed below.

Dichromats

Fig. 8 shows measurements made in the fovea upon the three types of dichromats. The results are in full agreement with previous experiments (Wald, 1966): the protanope lacks the red-sensitive pigment, the two deuteranopes lack the green-sensitive pigment, and the tritanope lacks the blue-sensitive pigment.

Figs. 9 and 10 show the results for the two deuteranopes at the 7°, 20°, 40°, 60°, 70°, and 80° loci. Comparable data for the protanope are shown in Fig. 11. We were able to make complete peripheral measurements for the tritanope only at 30° and 70° out; these are shown in Fig. 12. (Incidentally, if a tritanope develops red-green blindness as does the normal, that should make him totally color-blind by about 20°–30° out).

Except for the missing mechanisms, the three types of dichromat exhibit the same kinds of changes in receptor sensitivity as the normal trichromat. These relations are shown more clearly in Fig. 13. In both the deuteranope and protanope the blue-sensitive mechanism falls in sensitivity by almost 2.0 log units at the extreme peripheral loci compared with the 7° locus. The

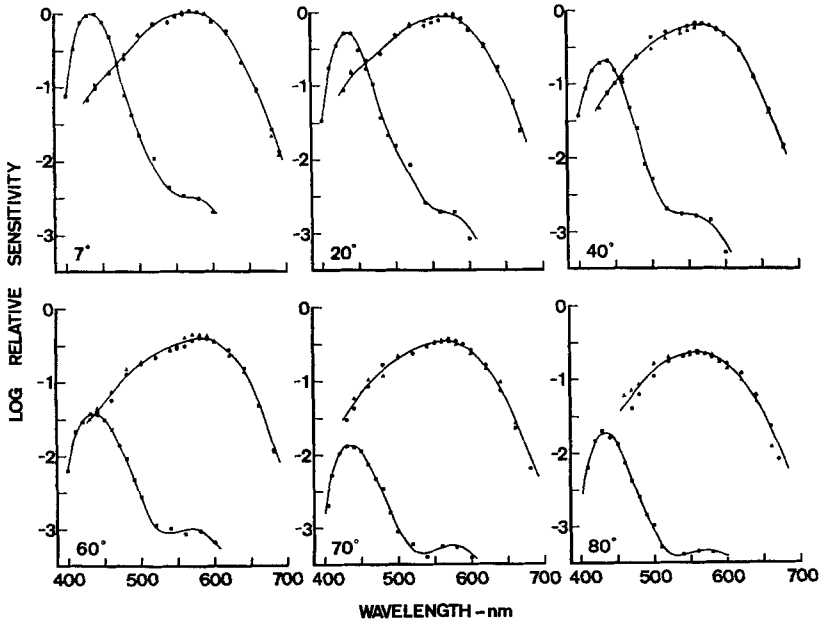

FIGURE 9. Spectral sensitivities of color mechanisms in peripheral fields of deuteranope B. C. The peak sensitivities are arbitrarily equated at the 7° locus. Symbols as in Fig. 3.

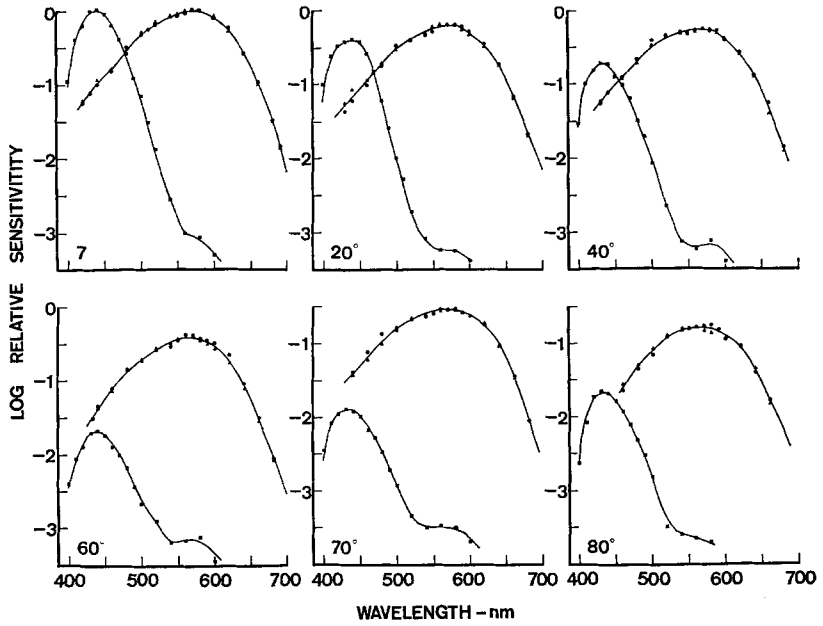

FIGURE 10. Spectral sensitivities of color mechanisms in peripheral fields of deuteranope P. C. Otherwise as in Fig. 9.

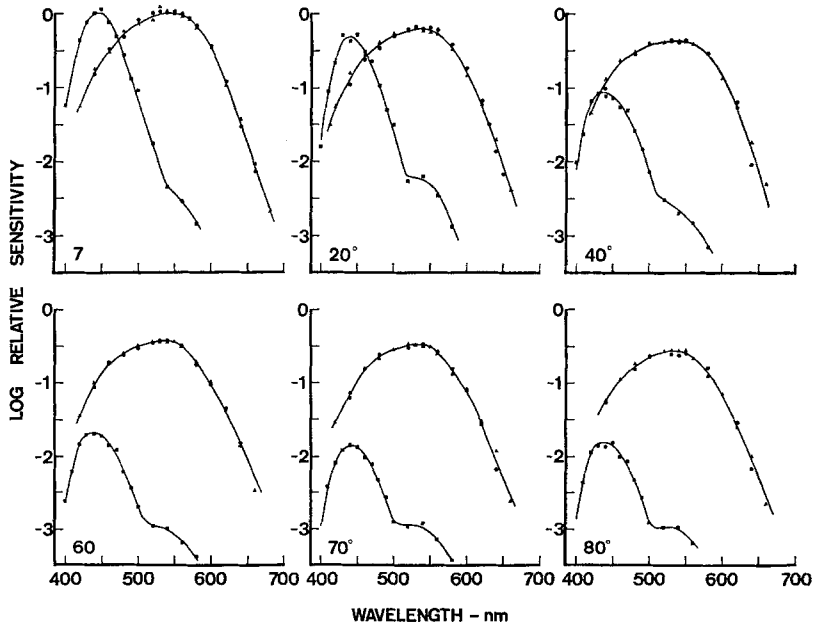

FIGURE 11. Spectral sensitivities of color mechanisms in peripheral fields of protanope J. H. Otherwise as in Fig. 9.

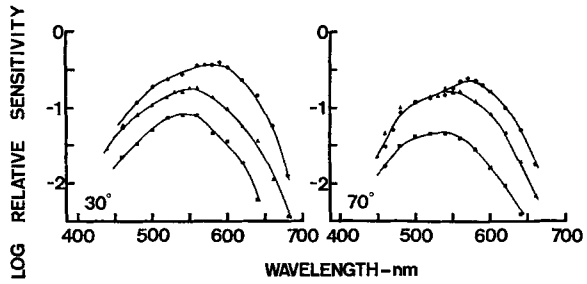

FIGURE 12. Spectral sensitivities of color mechanisms of tritanope R. B. as measured on yellow (squares), purple (triangles), and blue-green backgrounds (circles) at 30° and 70° from the fixation point.

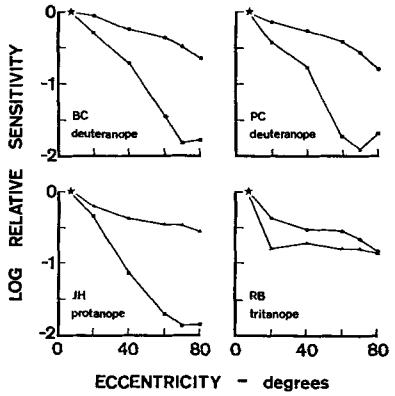

FIGURE 13. Peak sensitivities of the color mechanisms in peripheral fields of dichromats. Peaks arbitrarily equated at the 7° locus. The two color mechanisms present in dichromats change in sensitivity excentrically just as do the same mechanisms in trichromats. Compare Fig. 6. Symbols as in Fig. 3.

green-sensitive system in the protanope and the red-sensitive system in the deuteranope and both in the tritanope fall only about 0.7 log unit over the same range. We found no evidence in any of the dichromats that a color mechanism missing in the fovea is present in the periphery. All our observers with only two visual pigments functioning in the fovea have also only two functioning in the periphery.

DISCUSSION

Peripheral photopic luminosity function

The shape of the foveal luminosity function is usually thought to reflect (*a*) the spectral sensitivities of the three cone photopigments and (*b*) their weighted contributions. The blue-sensitive mechanism makes a relatively small contribution to foveal luminosity. In part this may be due to a relative paucity of

foveal, blue-sensitive receptors (Wald, 1967). Based on this line of reasoning, we would expect the cone luminosity function in the extreme peripheral retina to exhibit an even lower relative sensitivity to short-wave light since the blue-sensitivity curves for our observers show such a large decline in the periphery (Figs. 4–6).

Weale (1953 *b*), however, has measured peripheral luminosity functions and concluded just the opposite. Using a heterochromatic brightness matching procedure (with the retina light-adapted to a white of about 3.7 log trolands) he found that at 70° in the periphery the peak luminosity occurred in the blue at about 450 nm with a subsidiary peak at about 550 nm. He thought that his white surround was sufficiently bright to avoid any rod contribution, and that therefore the high blue sensitivity should imply a relative preponderance of blue-sensitive over red- and green-sensitive cones.

Weale's "white" adaptation light was produced by transilluminating laboratory filter paper with a tungsten lamp of unspecified color temperature. We have estimated the relative spectral energy distribution of such a "white" field by assuming the I.C.I. Source A and measuring the spectral transmittance of several types of filter paper. The dashed line in Fig. 14 shows these calculations after correction for the ocular media; the solid line shows the relative spectral energy at the receptor level of our yellow adaptation field. The bulk of the energy in Weale's "white" light is in the long-wave region of the spectrum and does not differ greatly from our yellow light. We conclude that the high blue sensitivity reported by Weale resulted largely from what was essentially a yellow adaptation field not unlike the one we use to isolate the blue-sensitive mechanism.

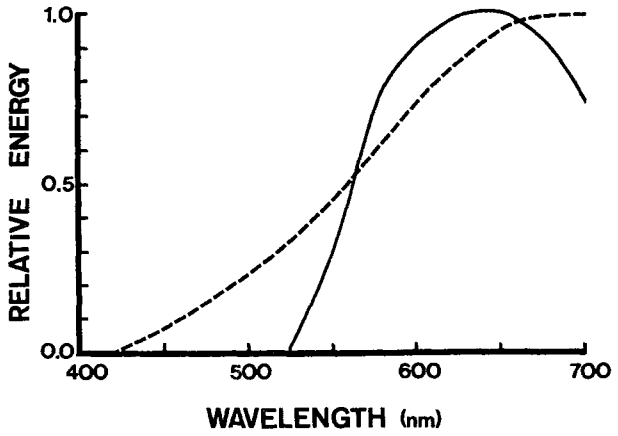

FIGURE 14. Relative energy distributions of yellow background used in the present experiments (solid line), and (broken line) such a "white" background as used for spectral sensitivity measurements in peripheral fields by Weale (1953 *a*).

Peripheral color zones

Though the many experiments that have attempted to characterize and delineate peripheral color zones have led sometimes to confusing and contradictory conclusions the substantial similarity between the hues seen by a normal trichromat in his mid-periphery and those seen by a congenital red-green blind dichromat in his fovea have suggested in the past that both might be caused by the loss of the green- or red-sensitive mechanism. The apparent monochromacy of the far periphery might then be caused by the loss of two of the three cone mechanisms. We have found, however, that all three foveal pigments occur all the way across the normal retina; or more generally that whatever photopigments function in the fovea persist to at least 80° peripherally.[5]

This suggests that the failure of color differentiation in the periphery may be ascribed to the convergence of afferent neural channels leading from the cones (i.e. a fusion rather than a reduction mechanism). Such neural fusion could occur at any level from retina to brain. Vilter (1949) reports that in the human retina the cone to cone-bipolar ratio changes from 1:3 in the central 20° to 1:1 beyond about 40°; this is at least a change in the right direction. At the subcortical level Polyak (1957) has demonstrated that the lateral geniculate nucleus is made up of six well-defined cell laminae in the area subserving central retinal regions but that they are fused into four or fewer laminae in the area subserving the peripheral retina. Talbot and Marshall (1941) and Cowey (1964) have demonstrated that the area of striate cortex devoted to the central visual field is much larger than the area that serves the periphery. So there are anatomical indications of greater convergence of neural pathways leading from the peripheral cones to the centers.

Our own observations seem to offer some internal evidence of neural fusion. If we suppose that the red- and green-sensitive mechanisms tend to share diminishing numbers of neural channels as the field moves further into the peripheral retina, that might help to explain why the *G* and *R* functions become more difficult to separate, and hence broader (Figs. 4 and 5). It is only *G* and *R* that raise such problems; *B* remains unaltered across the retina except for the increasingly prominent long wavelength tail, which is caused by the great decline in sensitivity of *B* peripherally, relative to *G* and *R*.

In order to quantify the separability of *R* and *G*, a new experiment was done. The log relative sensitivity was determined at 500 and 600 nm on the blue and on the purple backgrounds across the retina. To make the peripheral

[5] Weale's measurements of the photopic luminosity function in the peripheral retina by heterochromatic photometry (1953 *b*) tended to display maxima in the blue, green, and orange. Finding such maxima throughout the periphery to 70° led him to "suggest that three principal spectral mechanisms are present all over the retina."

and foveal data comparable, all the peripheral measurements were made with the xanthophyll filter before the eye, thus simulating the macular pigmentation throughout the peripheral fields. We then developed an "isolation index" for the degree to which *R* and *G* are separated. This is the difference between their log relative sensitivities at 500 nm when they are made equal at 600 nm. When the two systems are relatively well isolated, as in the fovea, this "isolation index" is about 0.8 log unit; but as the two functions become harder to separate the index grows smaller, reaching a value of zero when the two functions coincide at these wavelengths.

Fig. 15 (*a* and *b*) shows such measurements for the two normal observers. The isolation index remains constant at 0.8 at the fovea and at 7° out, where vision is still trichromatic. At 20° out, however, where red-green blindness is already evident, the isolation index has declined to about 0.3; and it continues to decline further, to about 0.2 at 80° out. The same tendency is apparent in our tritanope (Fig. 12). That is, the decline of separability of the *R* and *G* curves parallels to a degree the loss of red-green discrimination and eventually of all color discrimination.

By the same token, when the green-mechanism is isolated, as in our protanope, or the red-mechanism, as in our deuteranopes, the *G* and *R* curves do not change in shape or position throughout the periphery (Figs. 9–11). If

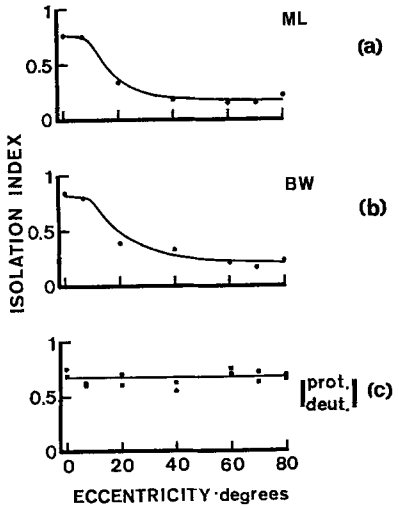

FIGURE 15. Isolation indices—a measure of the completeness of separation of the green- and red-mechanism—as a function of excentricity of field in two normal observers (*a*) and (*b*). (*c*), computed isolation indices for a hypothetical subject having the green-mechanism of protanope J. H and the red-mechanism of deuteranopes B. C. (circles) or P. C. (squares). (cf. Figs. 8–11). In (*a*) and (*b*) a xanthophyll filter placed before the eye simulated in peripheral fields the effects of the macular pigmentation in the fovea.

such *R* and *G* curves are put together to derive hypothetic isolation indices, the latter remain constant as the retina is traversed (Fig. 15 *c*).

We are left with the impression that whatever mechanisms account for red-green blindness in the presence of both the *R* and *G* systems involve also a tendency of the *R* and *G* curves to fuse.

Alternative possibilities that have occurred to us seem much less likely: for example, that the red- or green-sensitive photopigments broaden or shift in spectrum peripherally so as to overlap more widely and so be harder to separate. Changes in shape of spectrum are improbable; all the known vitamin A_1 visual pigments have nearly the same shape of spectrum when plotted on a frequency scale (Dartnall, 1953). That is true also of the human cone pigments (Brown and Wald, unpublished observations). Nor, as already said, do the *R* and *G* curves of the deuteranopes and the protanope, respectively, change in shape or position in the peripheral retina.

We think it most probable for all these reasons that the apparent color blindnesses of the normal peripheral retina have their main source in fusion mechanisms, involving the crossing and convergence of neural pathways from the cones to the centers, or even conceivably the occurrence of both the red- and green-sensitive pigments—perhaps in the far periphery all three cone pigments—in single cones. It may be that one needs to invoke such fusion mechanisms only in the red- and green-sensitive systems. Once they have fused to induce red-green blindness at 20°–30° out, that combined with the greatly lowered sensitivity of the blue-mechanism might be enough to induce total color blindness in the far periphery.

Such fusion mechanisms considerably reduce the varieties of color blindness in the normal retina. With the fusion of the red- and green-sensitive systems, one can no longer discriminate red- from green-blindness, protanopia from deuteranopia; there remains only the one condition, red-green blindness. Similarly, the apparent total color blindness of the far periphery is not a blue-, green- or red-cone or a rod monochromacy—all of which appear to exist in congenital forms of total colorblindness—but a single condition, the total failure of color vision in the presence of all four visual pigments and presumably the four types of receptor that contain them.

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